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CONTINUOUS AND DISCONTINUOUS VARIATIONS AND THEIR INHERITANCE IN PEROMYSCUS

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I. INTRODUCTION

MANY of the views which we are now accustomed to associate with the names of Weismann, Bateson, DeVries, Nilsson-Ehle and others were either foreshadowed or clearly formulated by Francis Galton, many years earlier. Galton's polygon, by which he illustrated the difference between continuous and discontinuous variations, is doubtless known to most readers; as is also his distinction between "blended" and "particulate" inheritance. It is less familiar, perhaps, that Galton regarded all inheritance as "largely, if not wholly, 'particulate.'" Even skin color, the classic example of blended inheritance in man, is presumably "none the less 'particulate' in its origin, but the result may be regarded as a fine mosaic too minute for its elements to be distinguished in a general view." Again, "the blending in stature is due to its being the aggregate of the quasi-independent inheritances of many separate parts" (1889, p. 139).

Galton did not deny all heritability to those variations which were represented by the minor oscillations of his polygon, although he refers to such variations as "unstable."

With the modern revival of Mendel's principles of

heredity and the definite formulation of a "mutation theory" of evolution, some of Galton's more or less tentative views have crystallized into dogmas. Along with the two just mentioned, there has been incorporated the principle of the "continuity of the germ-plasm," a conception which was likewise first clearly formulated by the great English geneticist, though its modern expression we owe to Weismann.

These various hypotheses have been woven together into a single fabric and made to reinforce one another. It will hardly be denied that some rather flimsy reasoning has been employed at times by those here concerned. Thus one familiar syllogism runs somewhat as follows: Somatic modifications are not inherited; fluctuating variations are not inherited; therefore fluctuating variations are somatic modifications. Indeed, "somatic" and "non-hereditary" have come to be used interchangeably by many writers. Whether or not somatic modifications ever become germinal is a matter to be settled by evidence. But I must confess that I have never regarded as self-evident the contention that because characters are found to be "non-hereditary" they are, *ipso facto*, "somatic" in origin.

A certain sanctity and inviolability has come to be attached to the units of heredity or "genes," according to the neo-Mendelian creed. Not only do these units refrain from any degree of blending, but—save for occasional mysterious "mutations"—they are quantitatively and qualitatively unchangeable. Thus, the only differences upon which selection, natural or artificial, can act are differences due to the presence or absence of different genetic factors. "We know," say the Hagedoorns, in an article (1917) which is typical of much of the recent literature of heredity, "that all the different genes, all the different inherited factors . . . are each in themselves invariable. . . . Liability to change by selection is synonymous with genotypic variability, and this true variability is synonymous with impurity."

Much dialectic skill has been displayed in maintaining this set of opinions against the many facts which seem directly to refute them. Indeed, it must be conceded that a fairly consistent and logical edifice has been erected upon these foundations. Strictly logical, though oftentimes improbable interpretations have been given to each new volley of hostile data, until the fortress has begun to seem impregnable—at least to a frontal attack.

But perhaps, of late, another metaphor has come to suit the situation better—that of the two knights fighting on opposite sides of the same shield. The Mendelians have recently had recourse to more and more minute factorial differences in explaining certain lesser gradations of color in some of their material, until at length the distinction between their opponent's "continuity" and their own "discontinuity" is more imaginary than real. Water is a continuous medium for all the ordinary purposes of life, and solutions of different substances may be completely "blended" therein. Its resolution into hypothetical molecules, atoms, electrons and the like does not in the least affect these fundamental facts.

The publication of the data which I offer in the present paper confessedly does not constitute a "frontal attack" upon the multiple factor hypothesis. My results belong to a class of facts which have already figured extensively in this controversy, and which have been met by ingenious and plausible counter-arguments. As I have stated elsewhere, I am led to doubt very seriously whether any *conceivable* evidence could be brought forward which would be admitted by the more extreme neo-Mendelians to be really damaging to their position. As in so many other cases, the victory is to be won, if at all, through a process of "attrition." Positions are gradually abandoned which are never *disproved* in a logical sense. Indeed, as hinted, above, there are clear signs that the defenders of the "multiple factor" explanation of selection and blended inheritance are already retiring from their main positions.

II. THE DISTRIBUTION OF SUBSPECIES

The term *subspecies,* as here employed, is nearly equivalent to *geographic race.* These subdivisions of a species occupy different, though often contiguous areas. When contiguous, they are said to intergrade completely with one another along the boundaries of their respective territories; and in any case, their ranges of variation overlap broadly. It is this fact, indeed, which leads to their being ranked as subspecies, rather than as distinct species, since the differences between some of the more widely separated among them would be quite sufficient to give them specific rank were there no connecting forms.

In such reports as those of Osgood on *Peromyscus* (1909), Nelson on the rabbits (1909), or Goldman on *Neotoma* (1910), the geographic ranges of certain species are seen to be divided up into what look like quite arbitrary subdivisions, corresponding to the ranges of the component subspecies. The boundaries between these subdivisions oftentimes follow certain natural barriers, but in some instances this does not appear to be true. And, in any case, it is doubtful whether any geographic barrier, save a continuous body of water or a lofty and unbroken range of mountains could prevent the free diffusion of such rodents. These minor areas, furthermore, frequently comprise territory having a very wide diversity of physical conditions. For example, *Peromyscus maniculatus gambeli* is represented as ranging from the foggy coastal area of central and southern California across the hot, semi-arid San Joaquin Valley to the snowy heights of the Sierra Nevada. And in latitude, its range is said to extend roughly from the 31st to the 48th parallel.

According to Osgood,

> Specimens from Monterey, the type locality, are absolutely identical with those from San Diego and the northeast coast of Lower California, and the intervening region is inhabited by exactly the same form. These, moreover, are like specimens from . . . the west slope of the Sierra (p. 69).

We might well be puzzled to discover any common ele-

ments of the physical environment which were responsible for the presence of the same subspecies under such widely divergent conditions of life. Particularly is this true when the environmental differences, as in the present case, far exceed those between the habitats of certain quite distinct subspecies.

Nor does the contention seem justified that such extensity in the distribution of a single subspecies is fully accounted for by the absence of any insurmountable barriers to its dispersal. So far as geographic features are concerned, the barriers between the range of *gambeli* and the ranges of certain neighboring subspecies seem to be no greater than some of those which traverse the territory of *gambeli* itself. Looking at the distribution maps in such publications as those just mentioned, one is impressed by a seeming analogy between the boundaries of these various subspecific ranges and those of the political subdivisions of the earth's surface. In considerable degree these last are bounded by geographic features, but to a large extent, also, the lines of demarcation seem to be drawn quite arbitrarily—the territories merely bound one another.

While great weight must be given to the findings of these taxonomic experts, I think it is our duty at present to accept certain of their conclusions with considerable reservation. This is particularly true of assertions as to the *absolute identity* of the characters of specimens from widely different parts of a given range. The published data make it plain that the authors are in no position to detect minor differences of a statistical nature. A small number of specimens from each locality are commonly compared, the measurements "in the flesh" of the various specimens necessarily having been made by a number of different collectors. It will be evident from the ensuing pages that the differences with which we are dealing are often of such a nature as to be revealed only by the comparison of large numbers of individuals, measured according to uniform standards. As regards the

latter point, tests which I have made of the standards of measurement employed by several competent collectors show clearly that the differences due to "personal equation" are sometimes at least as great as those which characterize quite distinct local races.

Accordingly, we might feel justified *a priori* in entertaining some skepticism as to the homogeneity of these races of animals throughout such great areas. Furthermore, I already have a certain amount of direct evidence which renders this contention improbable. Such evidence will be considered later.

An extremely desirable undertaking would be to run a series of trapping stations through the territories of two

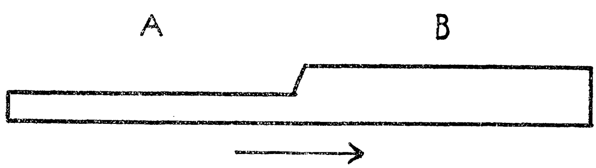

FIG. 1.

adjacent subspecies, at right angles to the supposed line of demarcation. This the author hopes to do in the course of time, though the task is not as simple as might perhaps be anticipated. Theoretically, a number of possible conditions might be revealed by such an investigation.

In the first place, it might be found (Fig. 1) that each of the two races was, in reality, "absolutely identical"

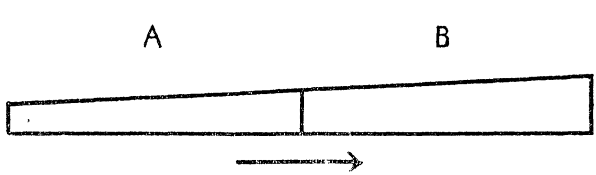

FIG. 2.

throughout its own range, while the transition between the two might be fairly abrupt.

Secondly, there might be an unbroken intergradation, in respect to the differential characters, throughout the

entire ranges of both the races (Fig. 2). In this case there would be no real boundary between the two groups, and indeed the recognition of two subspecies, rather than one or three, would be quite an arbitrary procedure.

Finally, there might be a condition, less easy to represent by diagrams, in which neither race was completely homogeneous, each being subject to considerable local variation within its own territory. Such local differences might or might not tend to be graduated as indicated in Fig. 2. Or, there might be some degree of gradation with respect to certain characters (*e. g.*, pigmentation), but not with respect to others (*e. g.*, length of appendages). In such circumstances, the recognition of two "subspecies" would depend upon the fact that the population of each of the respective territories was *relatively* uniform, and the changes encountered at the boundary *relatively* abrupt.

I am not yet in a position to say with certainty which of these possibilities is realized in the case of the species with which I am dealing (*Peromyscus maniculatus*), but I already have some strong evidence that the third one most nearly represents the actual state of arairs. As regards depth of pigmentation, we certainly find something approaching a graded series as we pass from the interior desert regions of California toward the coast, or as we pass from the coast of southern California, northward into successively more humid regions, as far as Alaska. But here we are dealing with a number of "subspecies." I have grounds for believing, however, that similar gradations occur within areas conventionally assigned to single subspecies.

Other questions of high theoretic importance relate to the nature of the animals inhabiting the so-called "areas of intergradation." Does this intermediate population manifest a complete blending of all the subspecific characters, or does it consist of a mixture of individuals, severally exhibiting the respective racial characters in a fairly pure state, or may there be a mosaic condition more

directly suggestive of Mendelian segregation? A definite answer to these questions I am likewise obliged to defer for the present.

Truly representative collections have been made by me thus far at only four stations within the State of California, though various other points have been visited and considerable numbers of the mice have been trapped there. My four principal collecting stations are located near Eureka, Berkeley, La Jolla and Victorville.[1] Meteorological records were kept for about two years at each of these points. These records have not thus far been carefully analyzed, however, so that their publication must be postponed. A preliminary comparison of climatic conditions at these four points has already been made (Sumner, 1915*a*). It will suffice, for present purposes, to state that, as regards both atmospheric humidity and rainfall, these stations rank (from highest to lowest) in the order given above, *i. e.*, Eureka, Berkeley, La Jolla and Victorville; while as regards mean annual temperature the reverse order holds.

The distribution of the three subspecies of *Peromyscus maniculatus*, recognized by Osgood as occurring within the limits of California, is represented in Fig. 3. It will be seen that one of my stations (Eureka) lies within the range of *rubidus*, another (Victorville) within the range of *sonoriensis*, while the other two (Berkeley and La Jolla) lie within the range attributed to *gambeli*.

In the ensuing pages, I am not in the least concerned with characterizing and defining those taxonomic groups which have been called *Peromyscus maniculatus gambeli*, *rubidus* and *sonoriensis*. I shall merely discuss the differences between (and within) four representative collections taken by me in widely separated and climatically different regions of the state. The question as to what "subspecies" a given mouse "belongs to" is for my purposes a distinctly minor consideration.

[1] Four other stations have been added since the present paper was written, but the data derived from these can not be included here.

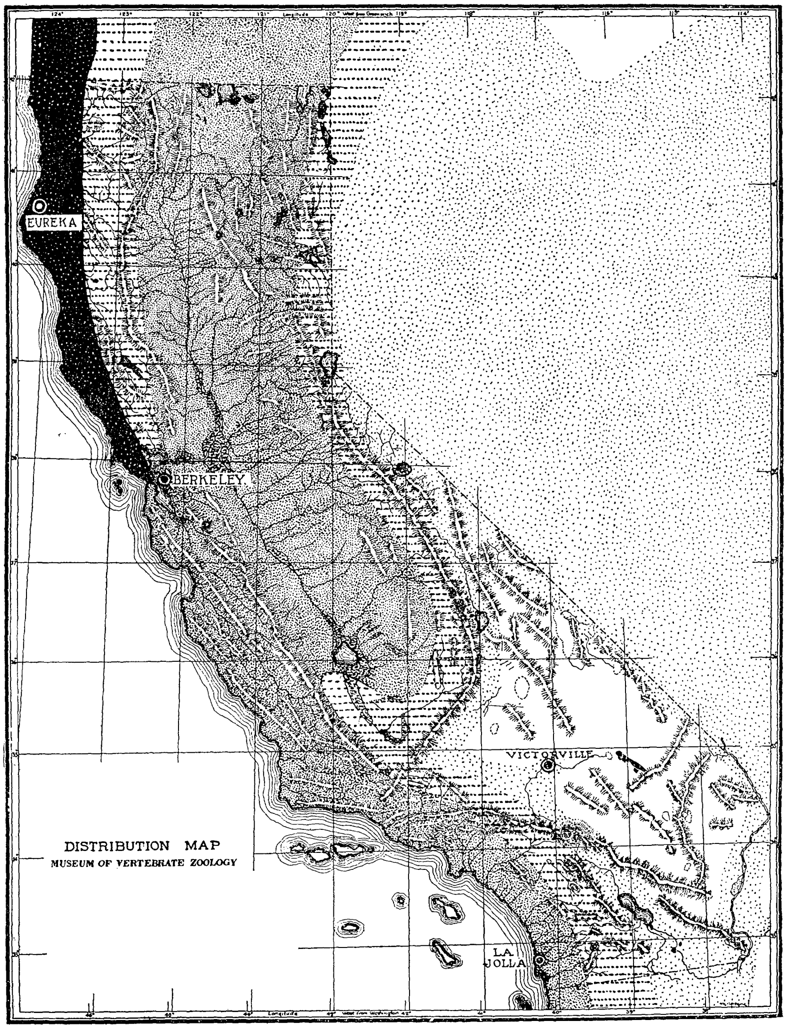

FIG. 3. Distribution of the recognized subspecies of *Peromyscus maniculatus* in California and Nevada, according to Osgood, 1909 (from Sumner, 1915). The heaviest shading denotes the range of *P. m. rubidus*, the intermediate shading that of *gambeli*, the lightest that of *sonoriensis*. Supposed areas of intergradation between two races are indicated by dotted lines.

III. Differences between the Four Local Races under Consideration[2]

These differences may be divided, for the sake of convenience, into pigmental and structural ones. Since the former are the most obvious, they will be discussed first.

1. *Pigmental Differences*

The pigmental differences relate to (1) the hair, (2) the skin.

Hair.—Like the other members of the genus *Peromyscus,* the mice of the present group are covered with pigmented hairs upon the dorsal and lateral surfaces, while the ventral surface and to a large extent the feet are covered with white hair. Upon the trunk these white hairs are, to be sure, devoid of pigment only at the distal ends. Parting the pelage at any point, dorsal, ventral or lateral, reveals the presence of a slate-colored basal zone in each hair.

The most obvious differences between the races under consideration relate to the dorsal coat color (Fig. 4). This is darkest in the animals from the humid redwood district (Eureka), palest in those from the Mojave Desert (Victorville), and of an intermediate hue in the collections from Berkeley and La Jolla. These last two races likewise differ from one another, the former being darker than the latter. Thus we have a series of four gradations, which are correlated directly with gradations in the rainfall and atmospheric humidity of their respective habitats.

It is important to notice, however, that these differences of shade relate rather to averages than to individual cases. *All* of the Eureka mice are not darker than *all* of the Berkeley mice. Nor are all of the Berkeley mice darker than all of the La Jolla mice, nor all of the latter darker than all of those from Victorville. In comparing repre-

[2] I here use the word "race" as being a non-committal term, elastic enough to cover any two collections of individuals which show significant differences of type.

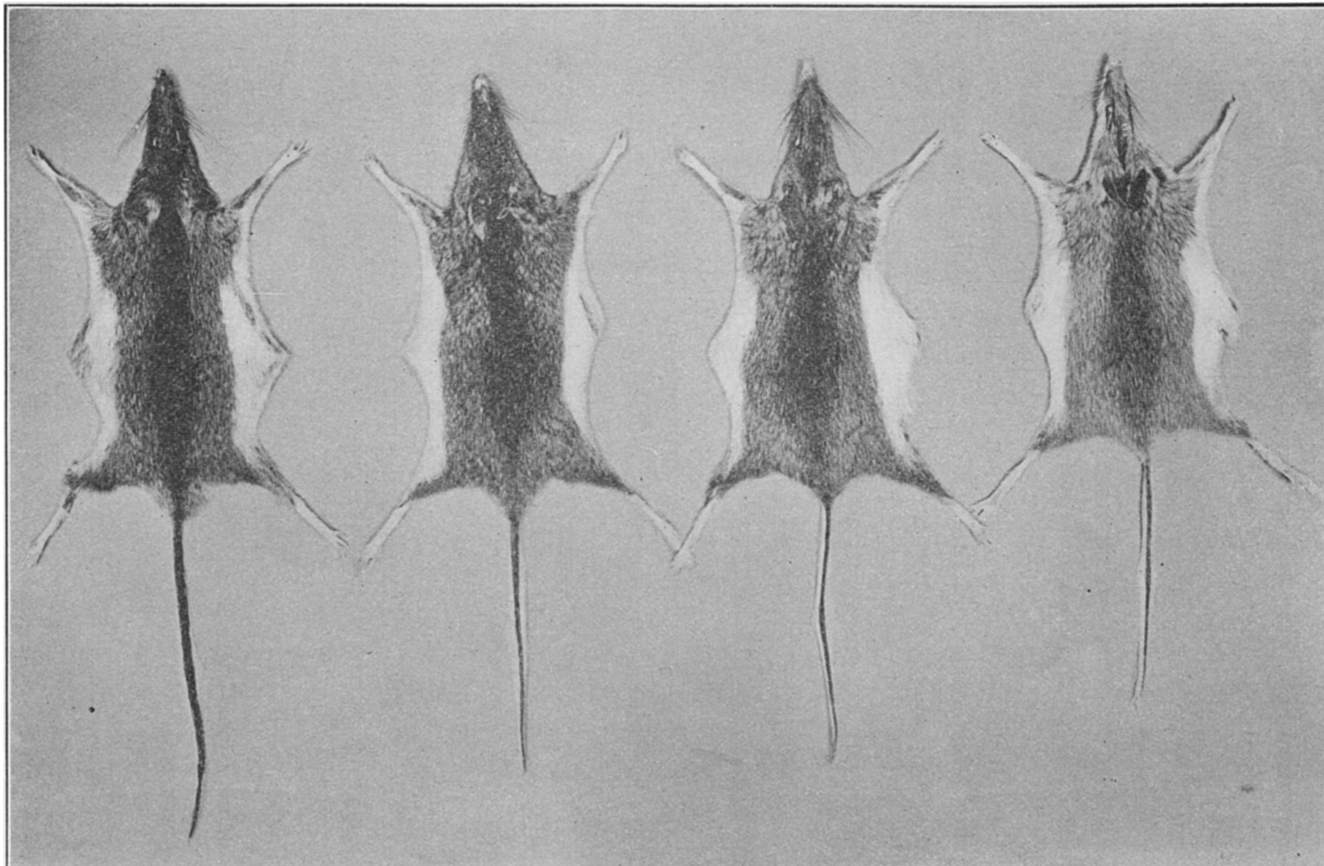

FIG. 4. Skins of male adult wild specimens of the Eureka, Berkeley, La Jolla and Victorville races of *Peromyscus maniculatus*, in order named. The skins have been selected with a view to showing the average shade of each series.

sentative collections of any two adjacent races belonging to this series, there is found to be a broad zone of overlapping. That is to say, there are many individuals in each set which, so far as color goes, could be equally well placed in either. I have, for example, laid out in parallel rows considerable numbers of *sonoriensis* and the La Jolla form of *gambeli*, and found that the darker half of the former set completely overlapped the paler half of the latter. While no confusion would be possible between the paler *sonoriensis* and the darker *gambeli*, there were a large number of specimens which could only arbitrarily be assigned to either "subspecies." Indeed, it is freely admitted by systematists that in many cases they can assign a given specimen to its proper subspecies only if they know the locality at which it was trapped. No such confusion would be possible, however, between the more divergent races of our series, *e. g.*, those from Eureka and the desert. I have never seen a *rubidus* which could not, by color alone, be readily distinguished from *sonoriensis* and vice versa.

Any attempt to give verbal equivalents for these color differences is highly unsatisfactory. In a later report I expect to undertake the analysis of these shades by means of a color wheel. For the present I will content myself with a very brief statement.[3] The dorsal darker stripe of the Eureka mice is of a shade lying somewhere between Ridgway's "sepia" and black, the paler lateral region lying between "Saccardo's umber" and "sepia."[4]

[3] The ensuing remarks apply only to the mature pelage. These mice pass through three distinct pelage phases: (1) the juvenal, which, in all races, is neutral gray in hue, and considerably darker than the adult shade; (2) the post-juvenal or adolescent, commonly paler and yellower than the last; (3) the mature or adult pelage, which is still more highly colored and frequently of still paler shade. The first molt occurs some time during the second month after birth, the second some time between the age of six months and a year. The various races of mice here considered, and even the mutants, are probably as clearly distinguishable in the immature pelages as they are in the adult.

[4] See Ridgway, 1912. "Dresden brown" and "mummy brown" perhaps approximate the shades in question as well as the last two mentioned.

Since the coat color is at no point homogeneous, any such comparison with uniformly tinted paper is of course very crude.

The desert mice are of a hue which can not even approximately be represented by reference to Ridgway's "color standards." The effect is probably not far from that which would result from a mixture of fine streaks of black and of "ochraceous buff" or "cinnamon buff," so proportioned as to approximate the general hue of the barren soil. As in all of these races, the mid-dorsal pelage is commonly darker than the lateral. All that need be said of the two collections of "*gambeli*" is that they are intermediate between the extreme types just referred to.

As a special case of the general hair color of the body, though not entirely correlated with this, is to be mentioned the color of the "ankle" region. The latter, particularly on its ectal surface, is covered with very short pigmented hairs, whose depth of shade affords another feature distinguishing the average condition of these four races.

I have given considerable attention to a microscopical examination of the hairs of these various mice. In position the pigment is of two different sorts, axial and superficial, located in the medulla and cortex respectively. A series of more or less disc-shaped, black pigment bodies extend from the base of each hair throughout the whole, or a considerable part, of its length. In the stouter hairs, there are, in the expanded region, two to four longitudinal rows of these bodies. In all cases, they alternate regularly with air spaces.

In the all-black hairs, the black pigment extends very nearly to the extreme tip. In the banded hairs, a region of varying length occurs in the distal half, in which the black pigment gives place to yellow. The dark pigment does not end abruptly, however. The dense black bodies become fragmented into their component rounded granules, as we pass from one segment to another, first giving

way to scattered collections of these granules (which are dark brown when seen singly) and later disappearing altogether. In the transitional region, black and yellow pigment may frequently be found in the same segment. In most hairs, the dark bodies again replace the yellow ones as we pass toward the tip; occasionally the yellow continues as far as any axial region is distinguishable.

The yellow pigment seems to be restricted to the axial part of the hair. To some extent, it occurs in the form of granules, but, unlike the black, it is largely present in a diffuse condition. This pigment is not all of the same tint, but varies in shade from a pale yellow to an orange or even a very pale brown.

For a varying length, on the distal, tapering ends of nearly all the hairs of the colored parts of the body, there is a very dark, granular pigment, lying close beneath the surface of the hair. This overlies and reinforces the axial pigment, so that the distal end is frequently darker than any other part of the hair. The superficial pigment, where dense, commonly looks almost black, but when seen in a thin layer the single granules appear brown. As already stated, this is likewise true, though in lesser degree, of the "black" axial pigment. In one of the "mutants," to be described later, this distal dark zone is nearly or quite lacking, and the same is true of certain exceptional samples of hair taken from normal individuals.

The yellow pigment is readily soluble in even fairly dilute potassium hydrate solutions, whereas the dark pigment is very much more resistant to this reagent, and may remain unchanged, even after the complete disintegration of the hair.[5]

Most students of this subject seem to follow Miss Durham (Bateson, 1903) in recognizing three pigments in the hair of *Mus musculus*—the black, the brown or chocolate, and the yellow. After considerable examination of the

[5] I have, however, observed preparations in which even the densest black pigment bodies assumed a reddish brown color, especially near the margin of the cover-glass.

hair both of *Mus* and *Peromyscus,* I can not feel sure of any sharp distinction between the black and the brown pigments. It is true that the axial pigment bodies of the basal portions of the hair are nearly dead black, while most of the superficial pigment at the distal ends is distinctly brown. But all gradations occur in the axial pigment of the transitional zones, and these gradations appear to be due not merely to differences in the density of the clusters of granules, but to gradations in the depth of color of the individual granules themselves. Without having made any careful chemical tests, I am disposed to believe that black and brown, in the hair of mice, are due merely to different degrees of aggregation of a single pigment. On the other hand, this dark pigment seems to differ, chemically and otherwise, from the various shades of yellow.

The differences in the color of mice of different subspecies and of different parts of the pelage of a single individual appear to be due to two chief causes: (1) the relative length of the pale zone, in relation to the rest of the hair; and (2) the proportionate numbers of the all-dark and of the banded hairs; probably also to (3) the depth of shade of the yellow pigment in the pale zones, and (4) the degree of concentration of the superficial pigment at the distal ends. In some of the "mutants," as will be pointed out below, certain other factors contribute to the differences shown.

Of importance for our general viewpoint is the fact that no one of the geographic races which has been examined possesses any type of hair which is wholly lacking in any other race. It would be impossible from a single hair, or even a small group of hairs, to say from what sort of mouse they were taken.

When viewed on the ventral side, these four races of mice likewise present characteristic differences. They form a graded series in respect to the whiteness of the pelage, which is purest in the desert race and least so in that from the redwoods. The differences are found to

result from the relative length of the terminal pigmentless zone which is present in these hairs. The ventral hair of the desert race also appears to be somewhat longer, or at least of a softer texture, than that of the others.

In the case of the ventral surface, like that of the dorsal, these differences relate to averages rather than to individuals. Likewise, it is of interest to note that within each race there is little or no correlation between the dorsal and the ventral shade. I have frequently graded a considerable row of mice of a single race in respect to the shade of the dorsal pelage, and found, on turning the animals over upon their backs,[6] that the order of arrangement did not correspond with the ventral gradations of shade.

Another differential character of these races is the degree of lateral extension of the ventral white area of the body, or, conversely stated, the ventral extension of the dorso-lateral pigmented area. The colored and uncolored regions of the body come together abruptly along an irregular lateral line extending from the snout to the tip of the tail. In the desert race, more of the white ventral region is usually to be seen in side view than is seen in the darker races. The gradation of the other three races among themselves is less obvious.

This degree of extension of the colored area relates not merely to the body but to the appendages. In the darker races an elongated tongue commonly extends down upon the fore-limb, in some cases even to the hand, while in *sonoriensis* such a ventral projection is usually little developed. The graduation of our four races in regard to this character corresponds to that noted in respect to shade. Similar conditions are observable on the hind limbs, particularly upon the ankle, where the pigmented hair may extend as far as the heel, or may fall short of this in varying degrees. The case of the tail will be discussed separately.

A hair character which seems to be peculiar to *sonoriensis,* among the races here considered, is the presence of

[6] Fresh specimens, not skins, are used for most of these comparisons.

small clusters of white-tipped hairs near the anterior insertions of the ears. But even this feature is not evident in all individuals.[6a]

Many species of *Peromyscus,* including the *maniculatus* series, have what is known as a "bicolored" tail. The hairs throughout a longitudinal stripe of varying width, upon the dorsal surface of this member are dark brown or black, while those of the ventral side are white. Now a casual inspection serves to show that this caudal stripe is broader and darker in the Eureka mice than in the desert ones, while a more careful comparison shows that the "*gambeli*" individuals are, on the whole, intermediate between the other two.

Fortunately, the breadth of this stripe is a character which may be subjected to fairly accurate measurement. It is my practice to slit the skin of the tail along the mid-ventral line, strip it off, and press the inner, damp surface firmly against a strip of black cardboard. The total width of this skin (= circumference of tail) is then taken at the mid-point of its length; likewise the width of the tail stripe. The ratio between the two readings is next determined, the width of the dorsal stripe being expressed as a percentage of the circumference of the tail. The following are the figures for the four races and the two sexes, the figure in parenthesis representing the number of animals measured:[7]

TABLE I

rubidus, ♂ (69)	42.51 ± 0.45
rubidus, ♀ (50)	41.96 ± 0.53
Berkeley *gambeli,* ♂ (24)	36.08 ± 0.80
Berkeley *gambeli,* ♀ (28)	35.50 ± 0.56
La Jolla *gambeli,* ♂ (85)	32.08 ± 0.33
La Jolla *gambeli,* ♀ (46)	32.43 ± 0.49
sonoriensis, ♂ (74)	27.49 ± 0.32
sonoriensis, ♀ (59)	28.92 ± 0.36

6a This condition I have recently found to occur in occasional specimens of *rubidus* trapped near Carlotta, California.

7 Since this character was not measured when these studies were first commenced, the number of individuals included in the present table falls far short of those measured for some other characters.

While the statistical certainty of these four types can not be doubted, it must again be insisted that the differences relate to averages rather than to individual animals. The frequency distributions of the various widths, as represented by the histograms (Fig. 5), show this point clearly. There is a certain amount of overlapping, even between the most divergent races.

Skin Pigmentation.—Certain regions of the skin are colored by dark pigment. The regions showing skin pigmentation most clearly are the ears, tip of snout, soles of feet, and, in the males, the scrotum.

Frequent comparisons of considerable numbers of freshly killed specimens have made it plain that, in respect to the pigmentation of the ears, our four races can be arranged in the same graded series as was found to hold for coat color. As regards the other three skin characters, I have never compared more than two races at a time, but I feel little doubt that all four could be arranged in the same order. No exact measurements are here possible, as in the case of the tail stripe. In a few instances I have, however, graded a given character, according to an arbitrary scale, and have thus been able to express the differences between two races in a roughly quantitative way. The following comparison between 42 *sonoriensis* and 38 La Jolla *gambeli* with respect to the pigmentation of the scrotum will illustrate this point.

TABLE II

	sonoriensis		*gambeli*	
	Number of Cases	Percentage	Number of Cases	Percentage
Heavy	1	2.4	3	7.9
Moderate	3	7.1	2	5.3
Slight	5	11.9	7	18.4
Very slight	1	2.4	4	10.5
None	32	76.2	22	57.9
Total	42	100.0	38	100.0

A similar tabulation was made in another case, comparing two lots of specimens of these same races in respect to the pigmentation of the foot.

It might readily be contended that all these various pigmental differences, which have thus far been considered, are merely manifestations of some general tendency toward a given degree of pigmentation of the body as a

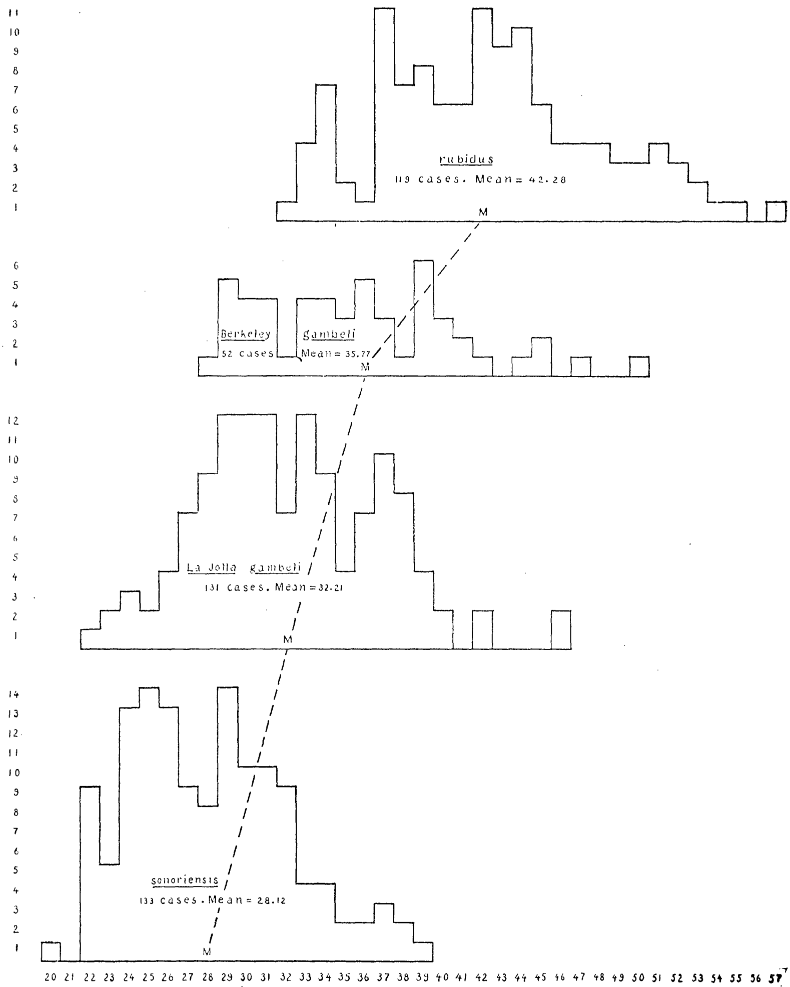

FIG. 5. Histograms, showing the frequency distributions of the percentage values for the width of the tail stripe (ratio to circumference) in the four races here considered (sexes combined).

whole. This tendency perhaps manifests itself in a greater or less intensity or extensity, or both. In the absence of exact quantitative standards, it is impossible

to determine whether or not these various pigment characters are correlated. If they are, the correlation is certainly not a close one, as frequent observations have shown. For example, the grade of foot-pigmentation was determined for the paler and darker halves of a series of *sonoriensis* and also for a series of *gambeli*. In both cases the average grade for the foot was slightly greater for the darker half than for the paler; but the difference was so small that I am not sure of its significance. Again, in the lot of 38 *gambeli* comprised in Table II the darkest individual (dorsally) and the one with the darkest feet were both devoid of visible pigment on the scrotum. Similar entries are frequent among my notes.

2. *Structural Differences*

The structural features which I have subjected to quantitative determination are (1) *weight,* (2) *body length,* (3) *tail length,* (4) *foot length,* (5) *ear length,* (6) *number of tail vertebræ;* together with several other skeletal characters which I shall not discuss in the present paper. The methods employed throughout these studies will be described more fully in a later report. A brief statement will suffice for the present. Body length, as here employed, is the total length, minus the length of the tail. In taking the total length, a special contrivance is employed, the body being stretched slightly and to a uniform extent. A constant procedure is likewise employed in measuring the tail length. The figure recorded for the latter represents the distance from the first free caudal vertebra to the tip of the tail, under a uniform degree of tension. The ear length here used is that from the summit of the "notch" to the tip of the ear. Foot length is the distance from the heel to the tip of the claw of the longest toe, the foot being pinned, sole downward, to a blackened board.

The statistical methods employed in analyzing these data have been rather fully discussed in a former paper (1915), to which the reader is referred.

(1) *Weight* and (2) *body length* are not dealt with directly in the present comparisons. The former is an index of metabolic condition as well as of size (*i. e.*, length). Captive mice, for example, are commonly fat in comparison with wild ones. *Body length* is of little significance in comparing two groups of mice, unless we know, either that the animals are all of the same age, or that the limit of growth has been reached by all of them. These things are frequently impossible to determine.

(3) *Tail length* is dealt with, both as an absolute value and as a percentage of the body length. If absolute tail lengths are to be compared in two groups of animals, the comparison can only be made between animals of approximately the same body length. My practise is to divide each series into a number of size-groups, differing by only two millimeters of body length. Group 80–81 of one series is then compared with group 80–81 of the other, group 82–83 with group 82–83, etc. The graphs (Figs. 6 and 7 and 9–12) are based upon this procedure. Each "curve" connects the means of the size-groups of each series of animals, the abscissas representing body length, the ordinates the character under comparison. In order to eliminate very young mice, groups having body lengths of less than 80 mm. are omitted. Even so, it is likely that most of the animals in the lower groups of the series are immature, but this fact in no way affects the validity of the comparisons.

It will be seen, from an inspection of the figures (6 and 7), for both males and females, that, as regards tail length, the Eureka mice (*rubidus*) stand in a class by themselves. In comparison with the wide interval between this long-tailed race and the other three races here considered, the latter differ but slightly among themselves. It is evident, none the less, that the La Jolla animals have somewhat longer tails than do those from Berkeley or Victorville, while the last two agree fairly closely in their mean condition.

Relative tail length, *i. e.*, the length of the tail expressed

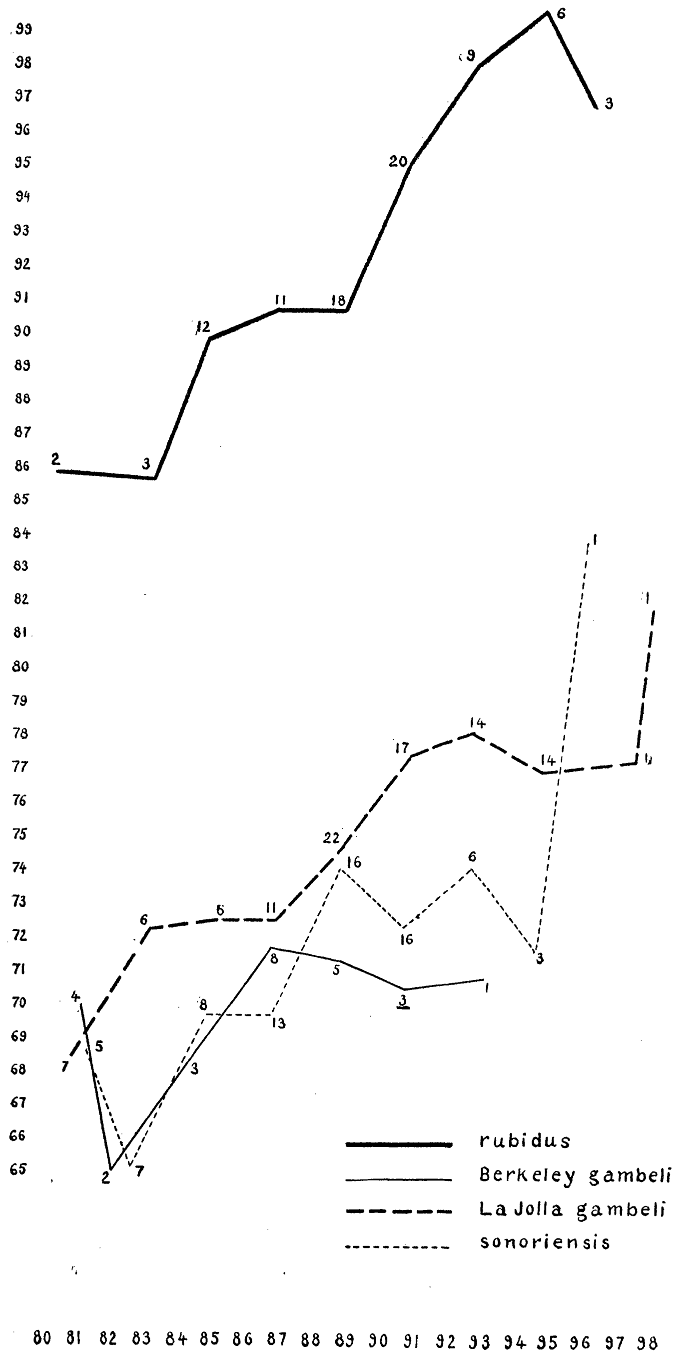

FIG. 6. Graphs for comparison of the absolute tail lengths in the four races (males). Abscissas denote body length; ordinates denote tail length; the figures along the "curves" indicate the numbers of individuals in the various size groups.

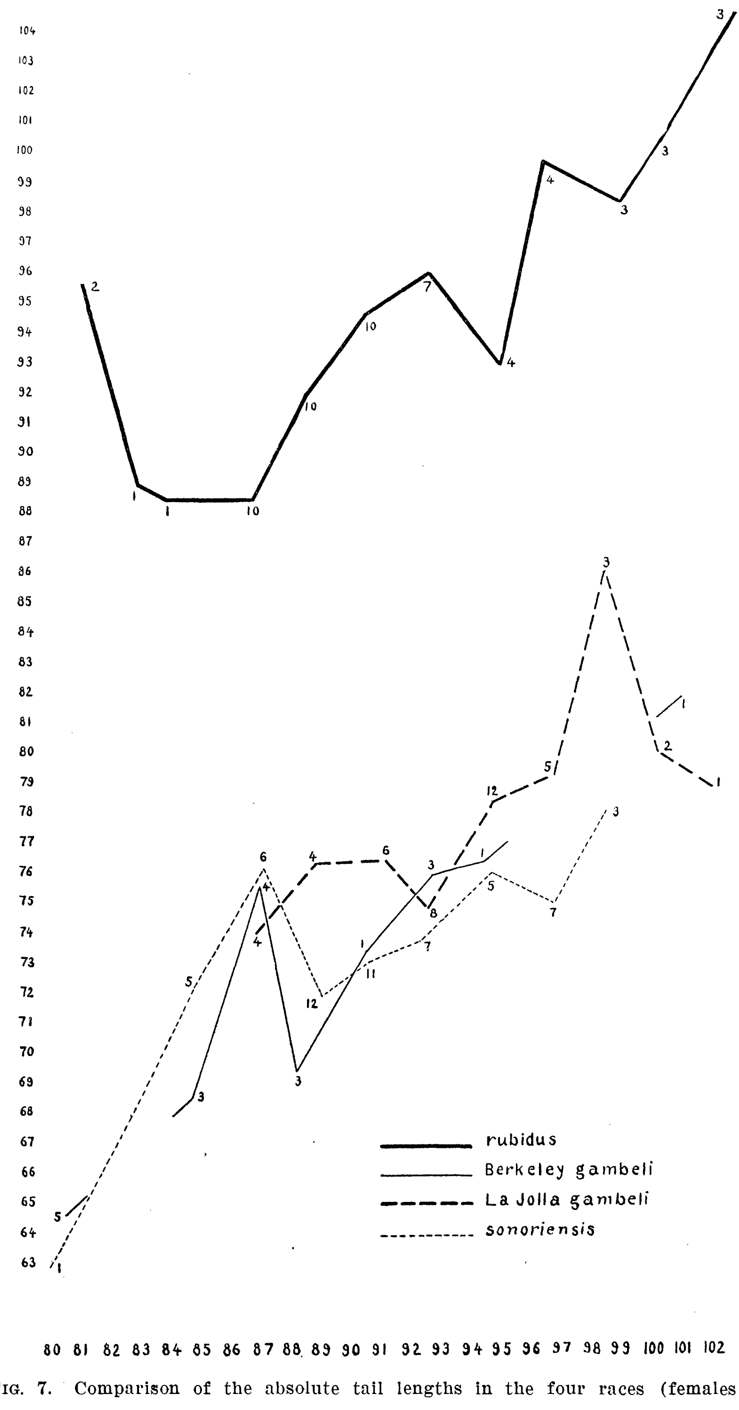

FIG. 7. Comparison of the absolute tail lengths in the four races (females).

as a percentage of that of the body, is to a considerable extent independent of the size of the animal. Larger mice, it is true, have relatively somewhat shorter tails than do smaller ones. But the differences are so slight that they may be overlooked, unless the mean size of the two groups under comparison differs considerably. The relative tail lengths of our four races of mice may be compared in the following table.[8] This shows the same relations as were portrayed by the graphs. It also shows that there are no significant differences between the sexes as regards the length of this member.

TABLE III

rubidus, ♂ (84)	104.45 ± 0.38
rubidus, ♀ (57)	103.37 ± 0.52
Berkeley *gambeli*, ♂ (26)	81.69 ± 0.55
Berkeley *gambeli*, ♀ (21)	81.76 ± 0.65
La Jolla *gambeli*, ♂ (99)	84.36 ± 0.35
La Jolla *gambeli*, ♀ (45)	83.04 ± 0.43
sonoriensis, ♂ (75)	81.29 ± 0.44
sonoriensis, ♀ (61)	81.30 ± 0.45

The distribution frequencies for these various lengths are represented by the histograms (Fig. 8). From these it is evident that only an occasional Eureka mouse has as short a tail as the longest tailed members of any of the other three races. The latter, however, differ from one another but slightly.

(4) In respect to *foot length* likewise (Figs. 9, 10) the Eureka mouse is very distinct from the other three races, while the latter show no significant differences among themselves. It is of interest, however, that in all four of these races the female has, on the average, a slightly shorter foot than the male. If any one still entertains the

[8] Owing to a slight change in the manner of measurement, which was made after these studies were commenced, the tail lengths of the earlier animals of my series have been rejected from the computations. This procedure has affected particularly the numbers of the Berkeley series.

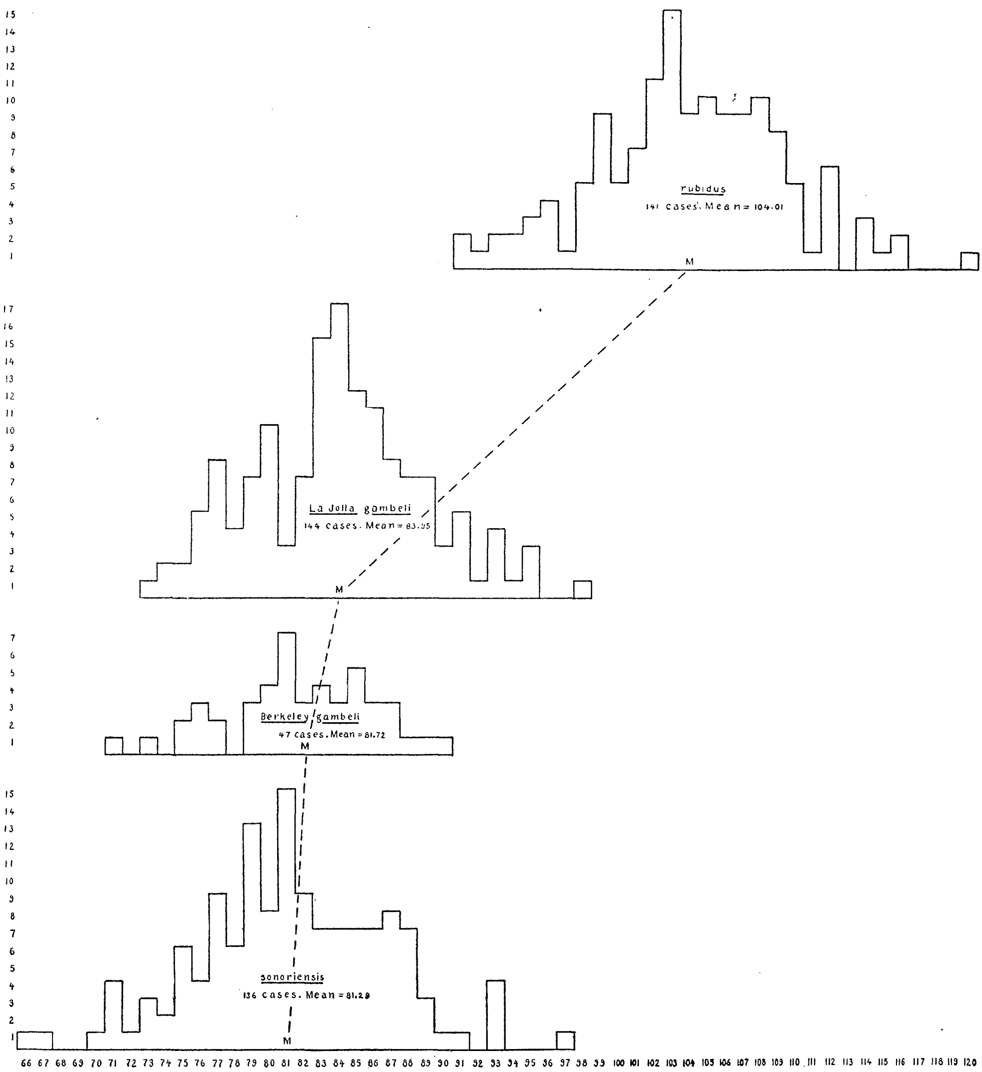

FIG. 8. Histograms, showing the frequency distributions of the percentage values for the length of the tail (ratio to body length), in the four races (sexes combined).

notion that small feet, along with other feminine charms in mankind, are due to "sexual selection," the situation in *Peromyscus* ought to give him pause.[9] The mean dif-

[9] This same difference was found by me to hold for white mice, at least for full grown individuals (1915, pp. 358, 367).

ferences between males and females, computed according to a method earlier described by me (1915, pp. 345, 346), are:

rubidus	0.31 mm. ± .08
gambeli (Berkeley)	0.29 mm. ± .05
gambeli (La Jolla)	0.09 mm. ± .07
sonoriensis	0.38 mm. ± .05

(5) In respect to *ear length,* we find a quite different set of relations. It is the La Jolla mouse in which these appendages are the longest, the Berkeley mouse in which they are the shortest, while the redwood and the desert animals occupy an approximately intermediate position and scarcely differ significantly from one another. It is here to be noted that the two extremes of the series, in respect to this character, have been placed by the systematists in the same "subspecies" (*gambeli*).

(6) The counting of the *tail vertebræ,* like the other measurements of skeletal characters, has not yet been completed. I have, however, determined the number in 25 specimens each of the Eureka, La Jolla and Victorville races. The fifth vertebra, counting from the most anterior one in the sacrum, has been regarded as the first of the caudal series. The averages and the frequency distributions are indicated in the following table.

TABLE IV

	23	24	25	26	27	28	29	30	31	Average
rubidus				2	9	6	5	1	2	28.0
gambeli (La Jolla)			4	5	13	3				26.6
sonoriensis	1	2	8	7	6	1				25.7

The significance of these differences seems highly probable, despite the small numbers. That between *rubidus* and *sonoriensis* can hardly be questioned. It seems plain, however, that the differences in tail length between these various races is not accounted for by the differences in the number of the vertebræ. Thus the Eureka mouse has a mean tail length which is 28 per cent. (of the smaller number) longer than that of the desert mouse. The pre-

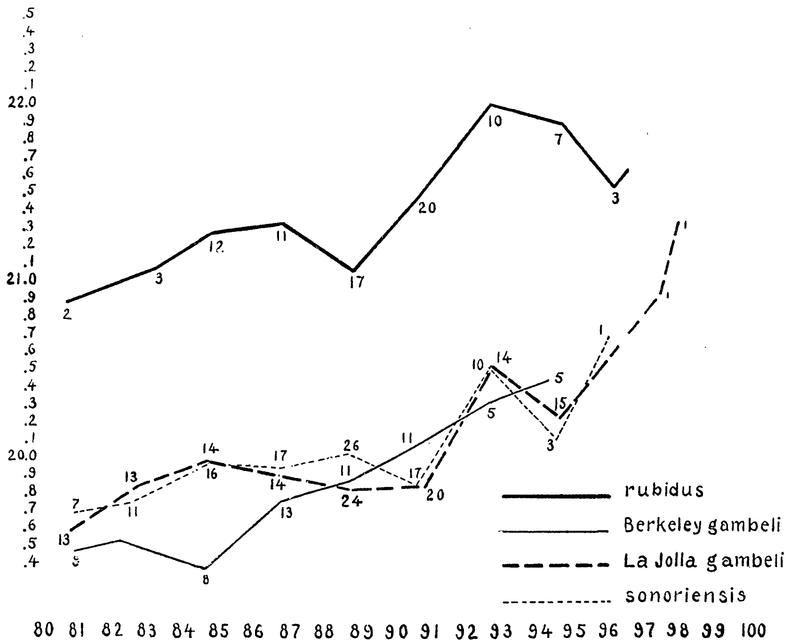

FIG. 9. Comparison of foot-lengths in the four races (males).

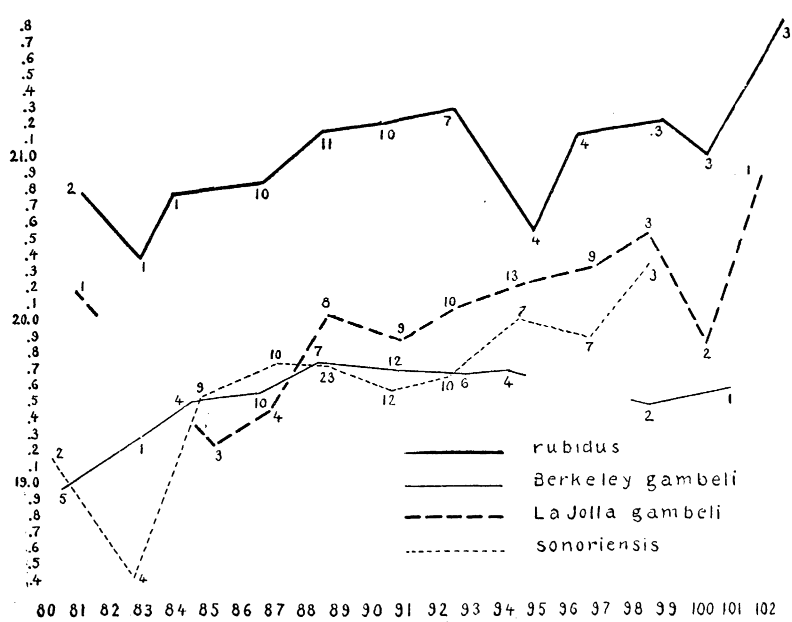

FIG. 10. Comparison of foot-lengths in the four races (females).

ponderance in the number of vertebræ is only 9 per cent. The differences in the length of this appendage are therefore due partly to the number of vertebræ, but chiefly to the length of the individual vertebræ.

Résumé of Racial Differences.—In relation to the vari-

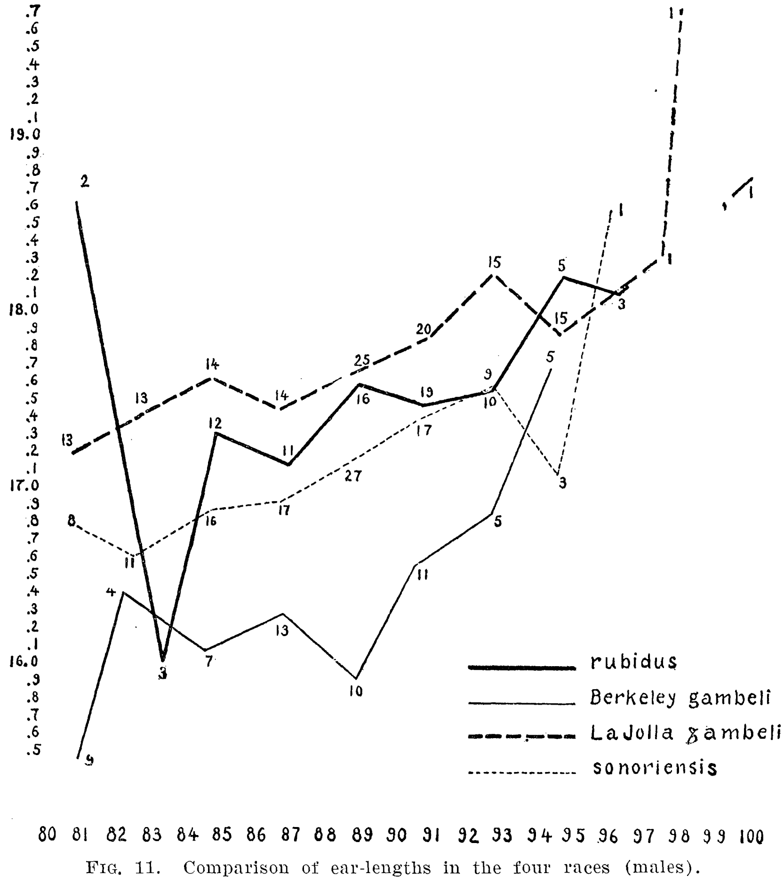

FIG. 11. Comparison of ear-lengths in the four races (males).

ous pigmental differences, those both of intensity and extensity, the four races under consideration were found to present the following graduated series:

Eureka > Berkeley > La Jolla > Victorville.

As regards the length to the tail, the series became:

$$\text{Eureka} > \text{La Jolla} > \begin{cases} \text{Berkeley,} \\ \text{Victorville.} \end{cases}$$

When the number of caudal vertebræ was considered, we had the same arrangement as the last for the three races for which determinations had been made, viz.:

Eureka > La Jolla > Victorville.

In respect to foot length, the following order held:

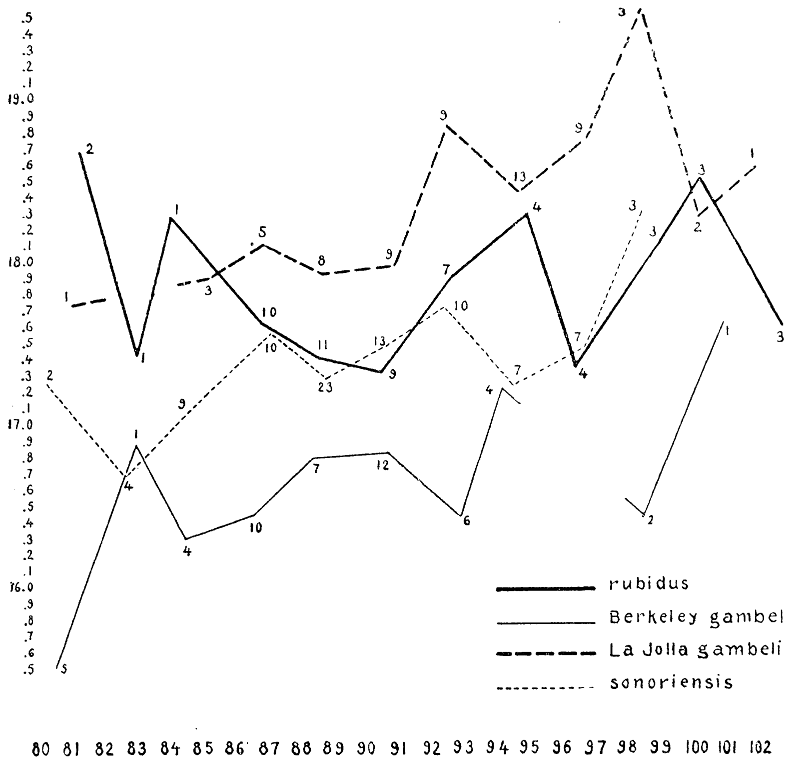

FIG. 12. Comparison of ear-lengths in the four races (females).

$$\text{Eureka} > \begin{cases} \text{La Jolla,} \\ \text{Berkeley,} \\ \text{Victorville.} \end{cases}$$

Finally, as regards ear length, we had a quite different alignment, viz.:

$$\text{La Jolla} > \left\{ \begin{matrix} \text{Eureka} \\ \text{Victorville} \end{matrix} \right\} > \text{Berkeley.}$$

It is plain that these "subspecies" have diverged from one another in respect to characters which have varied

quite independently. There is no single graded series for all the characters, which would lead us to suppose that they are in some way correlated or "linked" together.

When pigment characters alone are considered, the Berkeley mice are certainly intermediate between the La Jolla and the Eureka ones, and to that extent may be said to "approach *rubidus*."[10] But this is not true of the length of the tail, the foot or the ear. Indeed, as regards the first of these appendages, the Berkeley race diverges even farther from the Eureka race than does that of La Jolla.[11]

The question whether any of these various character differences may be physiologically or genetically linked together, so as to exhibit concomitant variations, is an interesting one, which I hope, in time, to treat rather fully. But I have already computed coefficients of correlation between two pairs of characters, viz.: between tail length and width of tail stripe, and between tail length and foot length.

In obtaining the former, I have based the coefficients upon the deviations from the mean *relative* tail length of each race and each sex, taken separately. Of these coefficients, three are positive and five negative. They range from -0.23 to $+0.09$, the mean being -0.03. Thus, it is plain that there is no appreciable correlation, within a single race, between the width of the tail stripe and the length of the tail, despite the fact that these characters seem to be associated, when certain darker races of the northwest coast are compared with more southward ranging forms.

There is, however, a quite marked correlation between the length of the tail and that of the foot. I do not here refer to the obvious fact that larger animals have larger

10 Osgood, 1909, p. 69. This author likewise states that Berkeley specimens are "longer-tailed than typical *gambeli*."

11 This conclusion is strengthened by consideration of an even larger series of Berkeley mice which were not included in Table III. The two sets were trapped in two different localities in the Berkeley hills.

tails and likewise larger feet than smaller animals. My figures show that, *even when animals of the same body length are considered,* those with longer tails tend, on the whole, to have longer feet, and vice versa. To obtain these results, I have computed the coefficients separately for each size-group, containing ten or more individuals.[12] All but 5 of these 21 figures are positive, the mean being + 0.27. Thus the greater tail and foot length of the Eureka race may have arisen simultaneously, both being the expression of a single constitutional change.

One further word regarding the nature of these racial differences, before we pass to a consideration of their heredity. It is plain that, with a single possible exception, all of the differences thus far considered are "substantive," rather than "meristic," to follow Bateson's[13] terminology, or "proportional," rather than "numerical," to use terms recently employed by Osborn.[14] In no case are they of the nature of "presence-and-absence" differences, such as figure so widely in Mendelian literature. Whether or not, on ultimate analysis, they can be resolved into the latter category, will be discussed later.

The differences without exception relate to means and modes, as was illustrated above by histograms constructed for two of the characters (Figs. 5 and 8). The frequency polygons commonly overlap broadly, when adjacent members of the series are compared. We find an approach to discontinuity only in a comparison of the most widely divergent races.

The single difference of a meristic or numerical character is that relating to the number of caudal vertebræ. But even here the difference is one of averages, for no single race seems to be characterized by the unvarying presence of any particular number of vertebræ, as certain larger taxonomic groups are characterized by a definite number of teeth or mammæ. It is worth mention also that

12 Cf. Sumner, 1915, pp. 349–350, 409–415.

13 1894, pp. 22, 23.

14 1915, p. 199. In the paper referred to, Osborn has given some attention to the case of *Peromyscus*.

the last one or two caudal vertebræ are commonly rudimentary, so much so that it is not always easy to determine their exact number. It is scarcely more fitting to apply the term "meristic variation" here than it would be to apply this term to such variations in the number of cells as distinguish a larger from a smaller foot or ear.

(*To be concluded.*)